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Inferring extinction from a sighting record

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Abstract

The extinctions of plant and animal species are almost never observed directly, but must be inferred from sighting records. This paper reviews some methods for statistical inference about the extinction of a single species based on a record of its sightings.
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1. Introduction

The earliest recorded sighting of the Caribbean monk seal (*Monachus tropicalis*) occurred in 1494 off the coast of Santo Domingo during the second voyage of Christopher Columbus. The last recorded sighting was in 1952 on the Seranilla Bank south of Jamaica. In 1977, a paper appeared entitled 'Caribbean monk seal extinct' [1]. Nine years later, a paper entitled 'The Caribbean monk seal is extinct' appeared [2]. Ten years after that, the Caribbean monk seal was formally declared extinct by the International Union for the Conservation of Nature [3]. Two years later, after conducting interviews with fishermen in northern Haiti and Jamaica, Boyd and Stanfield [4] concluded that 'it is possible that the Caribbean monk seal is not extinct'.

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As the case of the Caribbean monk seal illustrates, determining the fate of certain rare or cryptic species can be problematical. The purpose of this paper is to review some statistical methods for inferring the extinction of a species from the record of its sightings. In qualitative terms, the basic question is: How long must a species go unseen before it can safely be declared extinct? The answer to this question is not straightforward. The difficulty is that the answer depends on the expected rate at which the species would be seen were it not extinct. If this rate were very high, then even a relatively short lapse in sighting would indicate extinction. On the other hand, if this rate were very low, then even a relatively long lapse need not indicate extinction. Unfortunately, this rate, which is not necessarily constant over time, is unknown. The related problem of estimating the extinction time of a species known or assumed to be extinct is similarly not straightforward. The difficulty is again that a good estimate depends on the unknown pre-extinction sighting rate.

The paper is organized in the following way. In Section 2, a fairly general statistical model for a sighting record is described. Parametric methods for inferring extinction under this model are described in Section 3. Non-parametric methods are described in Section 4. As an example, the application of some of these methods to the sighting record of the Caribbean monk seal is presented in Section 5. Section 6 contains some concluding remarks.

2. A general model for a sighting record

Let $t_1 < t_2 < \cdots < t_n$ be the n times at which a species is sighted during the observation period $(0, T)$ ordered from earliest to latest. In the cases considered in this paper, the upper endpoint T of the observation period corresponds to the present time. In statistical terminology, such a sighting record can be modeled as a realization of a stochastic point process [5]. The first-order properties of a point process are characterized by a rate function $\lambda(t)$ that, roughly speaking, gives the mean rate of events (i.e., sightings) in a unit interval of time centered at t. In the case of a sighting record, the rate function reflects a combination of sighting effort and what might be called sightability (which, in turn, may reflect the abundance of the species). I will assume that, while the sighting effort can vary over time, it never falls to 0. The rate function describes only the first-order properties of a point process and is not a complete model. A fairly general model is the non-stationary Poisson process. Under this model, the numbers of events occurring in disjoint intervals are independent. I will also assume that the sighting record follows a non-stationary Poisson process.

Suppose that the species of interest becomes extinct at an unknown time T_E. In that case, the sighting rate $\lambda(t)$ will be positive for $0 \leqslant t \leqslant T_E$ and 0 for $T_E < t$. This paper is concerned with using the sighting record for statistical inference about T_E. In some cases, interest centers on testing the null hypothesis H_0 that extinction has not occurred (i.e., that $T_E \geqslant T$ or, equivalently, that $T_E = T$) against the alternative hypothesis H_1 that extinction has occurred (i.e., that $T_E < T$). In other cases, interest centers on providing a point or interval estimate of T_E. As discussed below, there is a close connection between a test for extinction and a confidence interval for extinction time. Specifically, the null hypothesis of no extinction cannot be rejected at significance level α if a $1 - \alpha$ confidence interval for extinction time covers the present time.

Inference about T_E is facilitated by the following result. For a non-stationary Poisson process with this rate function, conditional on the number n of sightings, the sighting record has the same

distribution as an ordered sample of n independent random variables with probability density function:

$$f(t) = \frac{\lambda(t)}{\int_0^{T_E} \lambda(u)\,\mathrm{d}u} \quad 0 \leqslant t \leqslant T_E. \tag{1}$$

The extinction time T_E plays the role of the upper endpoint of this distribution. Conditioning on n is advantageous because inference methods concerning a distribution endpoint are reasonably well-developed. These are discussed in the following two sections.

Before turning to specific cases, some remarks are in order about this formulation. First, it is assumed here that sightings are made in continuous time. In reality, most sighting records have a discrete resolution (e.g., annual). Provided that the observation period is relatively long in relation to its resolution, little is lost by adopting a continuous approximation. When time is treated as discrete, the possibility arises that multiple sighting occur in some periods. Under the model outlined above, the number of sightings within a discrete observation period has a Poisson distribution with mean given by the integral of $\lambda(t)$ over the observation period. Formal methods for inference about extinction time based on this kind of grouped data can be developed, but this is beyond the scope of this paper. Second, in many cases, it is not obvious when the observation period began. One way to proceed in such cases is to take the time of the first sighting as the beginning of the observation period (in which case, this sighting is omitted from the record). Third, although the non-stationary Poisson process model is quite flexible, it does assume that the sightings are independent. As a practical matter, this means that sightings that are obviously related should be combined.

3. The parametric approach

One approach to inference about the extinction time T_E is to adopt a parametric model for the pre-extinction sighting rate $\lambda(t)$ or, equivalently, for the probability density $f(t)$. For example, under the simplest model, the pre-extinction sighting record follows a stationary Poisson process with constant rate λ. In this case, which is considered in [6], $f(t)$ is the uniform density:

$$f(t) = \frac{1}{T_E} \quad 0 \leqslant t \leqslant T_E. \tag{2}$$

A natural statistic for testing H_0: $T_E = T$ against the alternative hypothesis H_1: $T_E < T$ is the time T_n of the most recent sighting, with H_0 being rejected for small values of T_n. In fact, it is straightforward to show that this is the likelihood ratio statistic for testing H_0 against H_1. The significance level (or p-value) of the observed value t_n of T_n is simply:

$$p = (t_n/T)^n. \tag{3}$$

The null hypothesis can be rejected at significance level α if this p-value is less than α. This procedure can be modified to test the null hypothesis that extinction occurred at a specified time T_0 against the alternative hypothesis that extinction occurred prior to T_0. The modification merely involves replacing T in (3) with T_0. This is used below in constructing a confidence interval for T_E.

Under the assumption that the species is extinct, the maximum likelihood estimate of the extinction time is the time t_n of the most recent sighting. This estimator is biased. A well-known result in sampling from the uniform distribution is that an unbiased estimate – in fact, the uniform minimum variance unbiased estimate – is

$$\widehat{T}_E = \frac{n+1}{n} t_n. \tag{4}$$

Under the assumption of extinction, the upper bound T_E^u of a $1-\alpha$ confidence interval for T_E of the form (t_n, T_E^u) can be found by inverting the significance level in (3). Specifically:

$$T_E^u = t_n/\alpha^{1/n}. \tag{5}$$

In words, this $1-\alpha$ confidence interval for T_E contains all hypothetical values T_0 of the extinction time that cannot be rejected by the α-level test with p-value given in (3).

The methods described so far assume that the pre-extinction sighting rate is constant over time. If the sighting rate declines prior to extinction (e.g., due to declining abundance), then these methods will be incorrect. Specifically, the p-value in (3) will be too small (i.e., too significant) and the point estimate $\widehat{T}_E$ in (4) and upper confidence bound T_E^u will be too small (i.e., too early). Solow [7] considered the case where the pre-extinction sighting rate declined exponentially at unknown rate β in time, in which case:

$$f(t) = \frac{\beta \exp(-\beta t)}{1-\exp(-\beta T_E)} \quad 0 \leqslant t \leqslant T_E. \tag{6}$$

This is called the truncated exponential distribution. In this case, the uniformly most powerful unbiased test of the null hypothesis H_0: $T_E = T$ has significance level $p = F(t_n)/F(T)$ where

$$F(x) = 1 - \sum_{i=1}^{[s/x]} (-1)^{i-1}, \binom{n}{i} \left(1 - \frac{ix}{s}\right)^{n-1}, \tag{7}$$

where $s = \sum_{i=1}^{n} t_i$ and [ ] denotes the integer part. Under the assumption of extinction, the minimum variance unbiased estimate of T_E is given by [8]

$$\widehat{T}_E = t_n + \frac{\sum_{i=0}^{[s/t_n]} (-1)^i \binom{n}{i} (s - it_n)^{n-1}}{n(n-1)\sum_{i=0}^{[s/t_n]-1} (-1)^i \binom{n-1}{i} (s-(i+1)t_n)^{n-2}}. \tag{8}$$

As before, a $1-\alpha$ confidence interval for T_E can be found by inverting the test described above. In this case, the inversion has to be done numerically. In some cases, the upper bound of this confidence interval does not exist. To put it another way, even for reasonable values of α (such as 0.05), it may not be possible to reject H_0 for arbitrarily large values of T. This problem, which is shared by some of the non-parametric methods discussed in the next section, makes it difficult to recommend this approach.

It is possible – at least in principle – to derive parallel results for other parametric models of the pre-extinction sighting rate. A delicate point in doing so concerns the choice of time origin $t = 0$. Briefly, in the uniform and exponential cases, this can be taken as the time of the first sighting, for

in these cases, the ensuing sighting rates remain uniform and exponential, respectively. This is not true of all models and it may be necessary to introduce an additional parameter to accommodate the unknown origin. A more fundamental objection to the parametric approach is simply that it can be difficult to justify a particular choice of model in a particular case. In the next section, some alternative non-parametric methods are reviewed.

4. Non-parametric methods

Certainly the simplest estimate of the upper endpoint of a distribution is the largest observed value t_n. This is clearly biased. A general non-parametric method for bias reduction is the jackknife introduced by Quenouille [9] and revived by Miller [10] – see also [11]. Robson and Whitlock [12] applied this approach to endpoint estimation and proposed the non-parametric estimate:

$$\widehat{T}_E = t_n + (t_n - t_{n-1}). \tag{9}$$

This estimate is extremely simple. The extent to which $\widehat{T}_E$ exceeds the under-estimate t_n depends on the sighting rate at the end of the record as reflected in the interval between the two most recent sightings. The estimate is exactly unbiased (but not efficient) when $f(t)$ is uniform, under-estimates T_E when $f(t)$ is declining in the neighborhood of T_E (as in the exponential case), and over-estimates T_E when $f(t)$ is increasing in the neighborhood of T_E. However, the bias in the latter two cases is smaller than that of the simpler estimate t_n.

Robson and Whitlock [12] went on the propose an approximate $1-\alpha$ confidence interval for T_E of the form (t_n, T_E^u) where

$$T_E^u = t_n + \frac{1-\alpha}{\alpha}(t_n - t_{n-1}) \tag{10}$$

and the corresponding p-value for testing for extinction is [13]

$$p = \frac{t_n - t_{n-1}}{T - t_{n-1}}. \tag{11}$$

Although the confidence interval based on (10) is robust, in the sense that its true coverage is close to the nominal value of $1-\alpha$, the interval itself can be quite wide and, in particular, much wider than the corresponding parametric interval. For example, in the case of a constant sighting rate, when $n = 10$, the 0.95 confidence interval based on (10) is, on average, around six times wider than that based on (4).

The endpoint estimate proposed by Robson and Whitlock [12] does not require knowledge of either the time origin $t = 0$ or the number n of sightings in the record. It also estimates T_E from the behavior at the end of the sighting record. From a statistical perspective, the general notion of basing inference about the upper tail of a distribution on only the largest observed values – in statistical terminology, the extreme order statistics – is attractive. This attractiveness is due to the result that, provided n is large (but not necessarily known), it is reasonable to assume that the joint distribution of the k most recent sightings $t_{n-k+1} < t_{n-k+2} < \cdots < t_n$ has the same parametric form – specifically, the Weibull extreme value distribution – regardless of the parent density $f(t)$ [14]. At least three approaches to inference about T_E based on the Weibull model have been proposed: a

likelihood approach [15], a minimum distance approach [16], and an approach based on optimal linear estimation [17]. Under the first two of these approaches, the estimate of T_E and the upper bound T_E^u of its confidence interval commonly do not exist. This problem is worse for the minimum distance approach than suggested in [16]. For this and other reasons, the approach proposed in [17] seems preferable.

The optimal linear estimate of T_E based on the k most recent sightings has the form:

$$\widehat{T}_E = \sum_{i=1}^{k} w_i t_{n-i+1}. \tag{12}$$

The weight vector $w = (w_1, w_2, \ldots, w_k)'$ is given by

$$w = (e'\Lambda^{-1}e)^{-1}\Lambda^{-1}e, \tag{13}$$

where e is a vector of k 1's and Λ is the symmetric k-by-k matrix with typical element:

$$\Lambda_{ij} = \frac{\Gamma(2\hat{\nu}+i)\Gamma(\hat{\nu}+j)}{\Gamma(\hat{\nu}+i)\Gamma(j)} \quad j \leqslant i, \tag{14}$$

where Γ is the gamma function and:

$$\hat{\nu} = \frac{1}{k-1}\sum_{i=1}^{k-2} \log\frac{t_n - t_{n-k+1}}{t_n - t_{i+1}} \tag{15}$$

is an estimate of the shape parameter of the Weibull extreme value distribution. An approximate p-value for testing for extinction is given by

$$p = \exp\left(-k\left(\frac{T - t_n}{T - t_{n-k+1}}\right)^{1/\hat{\nu}}\right). \tag{16}$$

Finally, under the assumption that the species is extinct, the upper bound of an approximate $1-\alpha$ confidence interval for T_E is

$$T_E^u = \frac{t_n - c(\alpha)t_{n-k+1}}{1 - c(\alpha)}, \tag{17}$$

where

$$c(\alpha) = \left(\frac{-\log\alpha}{k}\right)^{-\hat{\nu}}. \tag{18}$$

Roberts and Solow [18] applied these methods to estimate the extinction time of the Dodo (*Raphus cucullatus*).

A practical problem in applying this method – or any method based on the k most recent sightings – is the choice of k. This issue does not appear to have received a lot of attention. In qualitative terms, if k is too small, estimation under the Weibull model will suffer from the small sample size, while if k is too large, the asymptotic argument leading to the Weibull model may not hold.

5. An illustration

As an illustration of some of the methods described above, this section presents an application to the recent sighting record of the Caribbean monk seal. According to [2], reliable sightings were made in 1915, 1922, 1932, 1948, and 1952. This is a very sparse record and no method can be expected to perform very well.

Under the assumption of a constant pre-extinction sighting rate, taking the time origin to be 1915 (so that $T = 89$), and therefore omitting the initial sighting (so that $n = 4$), the p-value given by (3) is 0.03. By conventional standards, this suggests that H_0 can be rejected. Under the assumption that the species is extinct, the point estimate of T_E given in (4) is around 1961 and, from (5), the upper bound of the 0.95 confidence interval for T_E is around 1993.

Turning to the non-parametric jackknife method in [12], the p-value given in (11) is 0.07. By conventional standards, this would be considered as weak evidence against H_0. Under the assumption of extinction, the point estimate of T_E given in (9) is 1956. The upper bound of the 0.95 confidence interval given in (10) is 2028. This illustrates the relative inefficiency of this method.

Finally, suppose that the sightings listed above are actually the $k = 5$ most recent sightings in a much longer record. Adopting the Weibull extreme value model, the estimate of the shape parameter v given in (15) is 0.76 and the corresponding p-value in (16) is around 0.085. This is again weak evidence against H_0. Under the assumption that the species is extinct, the point estimate in (12) is around 1964 and the upper bound of the 0.95 confidence interval for T_E is around 2027. In essence, the results based on the Weibull model are less supportive of an early extinction than the results based on a constant sighting rate because the estimate of the shape parameter v is consistent with a sighting rate that is declining.

On the basis of these results, and given the small number of sightings, it is reasonable to conclude that the Caribbean monk seal is extinct, although the evidence of the sighting record is certainly not overwhelming.

6. Concluding remarks

The purpose of this paper has been to review methods for statistical inference about the extinction of a species based on the sighting record. The woods are not exactly full of papers in this area. This and only this explains the seemingly disproportionate number of references to my own work. Related work is described in [19] and [20]. By way of recommendation, limited experience suggests that the methods based on optimal linear estimation are a good overall choice and that this method works reasonably well when k is at least 5. The methods described in this paper may strike some as hopelessly formal and reductive. While there is something to this, my own view is that this kind of analysis provides a kind of quantitative check on more qualitative conclusions about extinction. Moreover, in some cases, the *only* information available – quantitative or qualitative – is a record of chance sightings.

One direction in which this work can be extended is toward inference about the extinction times of more than one species. This is of particular value in paleobiology (e.g., [21–23]) where there is considerable interest in mass extinction – i.e., a common extinction time for more than 1 taxon. In

this case, the sighting record for a species consists of the vertical stratigraphic locations of fossil finds. An issue in testing for mass extinction concerns the selection of taxa for inclusion in the analysis. The common practice of selecting taxa based on the stratigraphic height of the most recent find can badly bias tests in favor of detecting a mass extinction [24].

On the technical side, it would be useful to develop Bayesian methods for inference about extinction. Bayesian analysis under the uniform sighting rate model is discussed briefly in [6] using a so-called non-informative prior distribution. Of course, Bayesian methods are especially powerful when external information is available about extinction time or sighting rate. In related work, Ferraz et al. [25] adopted a Bayesian approach for inference about extinction based on annually grouped sighting data.

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